

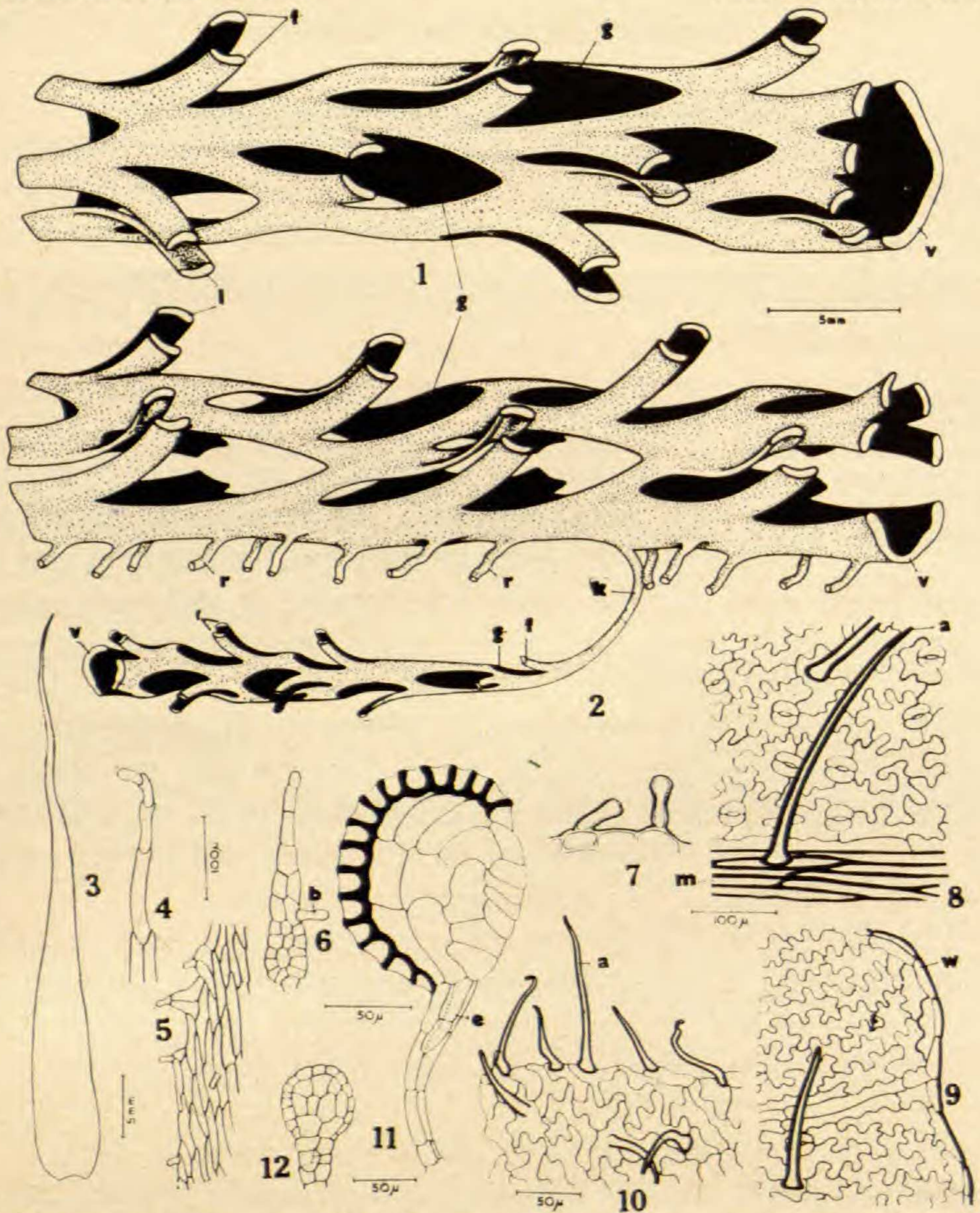
A Reinvestigation of the Morphology of *Hypodematium crenatum*

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Taxonomically as well as phylogenetically the small fern genus *Hypodematium* remains a problematic one. It includes the widespread, pantropic species *H. crenatum* (Forsk.) Kuhn and perhaps three or more other species, each of limited range in the China-Japan region; some pteridologists detect as many as 16 species. The genus has been associated with the woodsoid, tectarioid, athyrioid, and thelypteroid ferns by different taxonomists, and in some cases even by the same taxonomist at different times. Morphologically the genus is little known except for some aspects of *H. crenatum* published by Hayata (1927), Mehra and Loyal (1956), Loyal (1960), and Iwatsuki (1964a, b). Since the descriptions of these authors contain some discrepancies, we thought it worthwhile to reinvestigate the morphology of *H. crenatum* and to see whether the morphology of this plant could yield some additional clues as to the relationships of the genus.

Material for this study was collected growing in rock crevices from Chakrata (Central Himalaya) and was then cultivated in the fernery of the National Botanic Gardens. Spore morphology was studied using standard palynological techniques, as described by Nayar and Devi (1964). Prothalli were grown on sterilized nutrient agar medium in petri dishes maintained at $24 \pm 2^\circ \text{C}$ and at about 600 ft-c light intensity, as described by Nayar (1962). The light source was fluorescent "day light" lamps for 12 hours in each day. Vascular organization of the rhizome was studied from steles excavated mechanically from the rhizome, as well as from reconstructions based on camera lucida drawings of serial microtome sections.

THE RHIZOME is thick, creeping, cylindrical, bears several dormant branches on the ventral surface, and is densely covered by basally attached, golden brown, lanceolate, thin-walled paleae about 30×3 mm (*Fig. 3*) mixed with profuse, unicellular, papillate, glandular hairs (*Fig. 7*). The apex of the palea is uniseriate and



MORPHOLOGY OF THE SPOROPHYTE OF *HYPODEMATIUM CRENATUM*. FIG. 1. VASCULAR CYLINDER OF A PORTION OF THE RHIZOME, DORSAL VIEW. FIG. 2. SAME, LATERAL VIEW. FIG. 3. MATURE PALEA. FIG. 4. SAME, APEX. FIG. 5. SAME, MARGIN. FIG. 6. IMMATURE PALEA AT STAGE MARGINAL HAIRS ARE PRODUCED. FIG. 7. PAPILLATE HAIRS ON RHIZOME. FIG. 8. LOWER LEAF EPIDERMIS. FIG. 9. UPPER LEAF EPIDERMIS. FIG. 10. PORTION OF INDUSIUM SHOWING ACICULAR HAIRS. FIG. 11. MATURE SPORANGIUM. FIG. 12. IMMATURE SPORANGIUM SHOWING ORIGIN OF THIRD ROW OF STALK CELLS. The abbreviations are: a = ACICULAR HAIR, b = GLANDULAR HAIR, e = SECONDARY ROW OF STALK CELLS, f = LEAF TRACE, g = LEAF GAP, k = BRANCH TRACE, m = CELLS OVER VEIN, w = MARGINAL CELLS, r = ROOT TRACE, and v = VENTRAL MERISTELE.

is terminated by a non-glandular, barrel-shaped cell (*Fig. 4*). Young paleae bear sparse, unicellular, papillate, glandular hairs (*Fig. 5*) on the margin and both surfaces. The hairs are formed early during development of the paleae, sometimes when the paleae are only three cells broad (*Fig. 6*), and are deciduous. Filamentous, marginal protrusions bearing hairs are found occasionally on the basal region of the paleae. The rhizome is parenchymatous, with small, globose or ovoid masses of thick-walled cells with dark brown contents scattered irregularly in the ground tissue. In rhizome transections these sclerenchyma masses appear like the sclerenchyma strands found in many dryopteroid ferns, but they are not elongate strands. The vascular cylinder of the rhizome (*Figs. 1, 2*) is distinctive and, as reported by Mehra and Loyal (1956) and Iwatsuki (1964a, b), has a broad, undivided ventral half and a dissected dorsal half, recalling that of the Lomariopsidaceae (Nayar & Kaur, 1965). In the adult rhizome there are generally three irregular rows of leaf gaps dissecting the dorsal half of the stelar cylinder—not two alternating rows, as reported by Iwatsuki (1964a, b). The leaf gaps are clearly arranged in a spiral around the vascular cylinder, with a larger distance between successive gaps on the ventral side. The lateral leaf gaps are markedly displaced towards the dorsal median plane. The leaf gaps are large and spindle-shaped and dissect the dorsal half of the stele into narrow, ribbon-like vascular strands. Leaf traces (*Figs. 1, 2, f*) are paired, ribbon-like strands, and the leaf gap extends conspicuously on the abaxial as well as on the adaxial side of them. Root traces are restricted to the ventral, undissected portion of the stele, and originate as thick, superficial, cylindrical branches; they are not associated with the leaf gaps. Branch traces (*Fig. 2, k*) are profuse and are restricted to the ventral half of the stelar cylinder. They are similar to the root traces in being cylindrical, solid strands arising superficially on the stelar surface (not associated with any branch gap) and oriented in the same way (not at the margins of the ventral meristele, as Mehra and Loyal (1956) reported). While passing through the cortex of the rhizome, the branch trace becomes medullated and at the branch base it is

siphonostelic. In developed branches it becomes dissected into a radially symmetrical dictyostele with spirally arranged leaf gaps, but as the branch thickens and grows away from the main rhizome, the ventral leaf gaps become displaced and the ventral half of the vascular cylinder becomes undissected. The xylem tissue of the vascular cylinder is massive and often has 10–12 rows of tracheids that are liberally mixed with thin plates of xylem parenchyma. The phloem forms a thin sheath around the xylem, but is discontinuous at the region of the leaf gaps (margins of the ribbon-like meristemes). The pericycle is three- or four-layered, and the endodermal cells occasionally have faintly thickened inner walls.

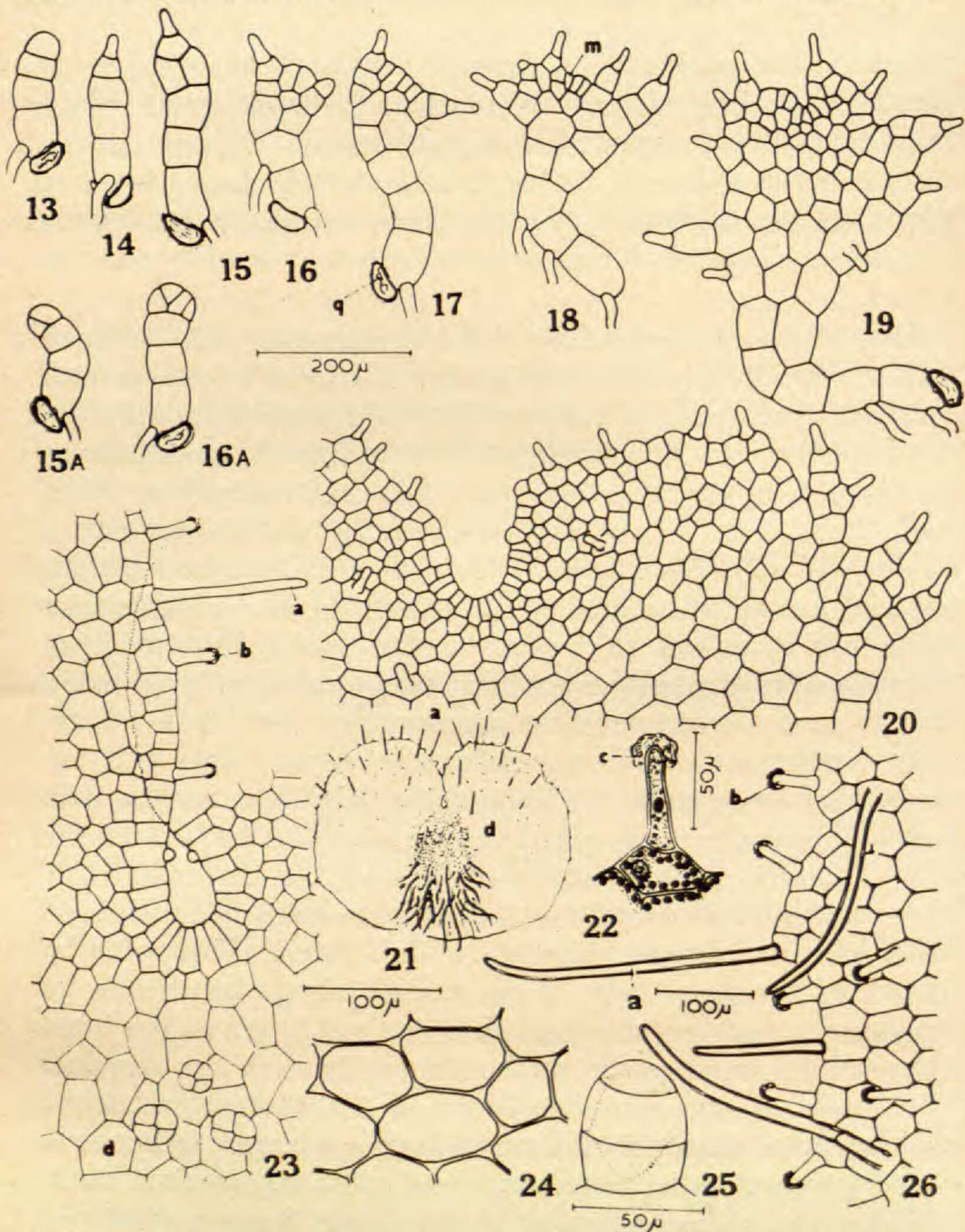
THE LEAVES are crowded, with the leaf bases persistent and densely aggregated on the dorsal surface of the rhizome. The leaf bases are conspicuously swollen and tuberous, as reported in *Pteris wallichiana* (Chandra & Nayar, 1970). Many of the lateral leaves are undeveloped except for their swollen bases; the upper part of such leaves is represented by a deciduous, hump-like protrusion. The swollen leaf bases bear profuse paleae and unicellular hairs. They are parenchymatous like the rhizome and possess scattered sclerenchyma masses; dense deposits of starch occur in the parenchyma cells. The stipe above the swollen base is sharply delimited, nearly cylindrical, and hard due to a broad hypodermal sheath of 5–8 layers of very thick-walled cells. The epidermis is thin-walled and bears unicellular hairs. Sclerenchyma masses are absent in the stipe. The vascular supply consists of a pair of broad, laterally placed strands, with the inner walls of the endodermal cells conspicuously thickened and dark brown. The leaves are shed where the stipe joins the swollen leaf base, but, as noted by Iwatsuki (1964a, b), there is no clear abscission tissue such as occurs in ferns with distinctly articulated leaves (e.g., the Polypodiaceae). A layer of cells of the stipe next to the swollen base turns brown in the old leaves and ultimately shrivels up, resulting in the shedding of the anterior part of the leaf.

The rachis and its branches are subterete with a more or less flat adaxial surface. The two vascular strands of the stipe fuse by their abaxial margins into a solitary bundle, which is nearly

trigonal in the anterior half of the rachis. Xylem tissue of the rachis, bundle is deeply adaxially channeled (U-shaped), with broad, thin, prominently incurved, flap-like margins. Phloem entirely surrounds the xylem in a thin sheath, and the pericycle which surrounds the phloem is one cell thick, except on the adaxial side, where it is much thicker and fills the concavity of the vascular strand.

The lamina is herbaceous and decomposed. The ultimate segments are oblong, with blunt apices and a broadly lobed margin. Venation is pinnate, with pinnately branched main lateral veins corresponding to the marginal lobes. Elongate, unicellular or occasionally bi- or tri-cellular, acicular, achlorophyllous, thick-walled hairs, often with peg-like protuberances on the inner surface of the cell wall (*Fig. 8*), are found all over the lamina, more profusely on the veins and axes. Epidermal cells of the lamina, other than those over the veins, are thin-walled, chlorophyllous, and with a broadly sinuous contour; cells of the lower epidermis have a more conspicuously sinuous outline than those of the upper epidermis. Epidermal cells over veins (*Figs. 8, 9, m*) on both surfaces differ in being achlorophyllous, narrow with a smooth contour, and conspicuously elongate parallel to the vein. Similarly, the cells at the margin of the lamina (*Fig. 9, w*) are achlorophyllous, with smooth contour, thickened peripheral walls, and are elongate parallel to the margin. This band of specialized marginal cells is continuous along the margin of the pinnules and becomes more than one cell broad at the basal region of the pinnules and at the sinuses between the marginal lobes, recalling the sinus-membrane of the thelypteroid ferns. The bands of elongate, achlorophyllous epidermal cells above the veins extend to the margin and merge with the marginal band.

THE SPORANGIA are produced in circular sori borne medianly on the lateral veinlets. The sorus is protected by a deeply reniform, basally attached indusium composed of a single layer of cells resembling the cells of the foliar epidermis. Acicular hairs similar to those on the lamina, but often having hooked apices, are profuse on the outer surface as well as on the margin (*Fig. 10*); the marginal



MORPHOLOGY OF THE GAMETOPHYTE OF *HYPODEMATIUM CRENATUM*. FIGS. 13-19. STAGES IN PROTHALLIAL PLATE DEVELOPMENT. FIG. 20. APEX OF YOUNG CORDATE PROTHALLUS. FIG. 21. ADULT PROTHALLUS. FIG. 22. MARGINAL PAPILLATE HAIR. FIG. 23. ADULT PROTHALLUS, APEX. FIG. 24. SAME, WING CELLS. FIG. 25. ANTHERIDIUM. FIG. 26. ADULT PROTHALLUS, ANTERIOR MARGIN WITH HAIRS. The abbreviations are: a = ELONGATE RHIZOID-LIKE HAIR, b = PAPILLATE SECRETORY HAIR, c = EXTRA-CELLULAR SECRETION, d = ARCHEGONIA, and q = SPORE COAT.

hairs often are larger than the superficial ones. Sporangia (*Fig. 11*) are the typical leptosporangiate type, with a long stalk composed of four tiers of elongate cells. The stalk is two cells thick, with the rows contiguous with either end of the annular ring, except at the capsule base, where there is a third row two cells long formed secondarily during sporangial development as a downward outgrowth of the basal cell of the capsule wall on one of its flat sides (*Fig. 12*). The annulus consists of 16–20 indurated cells.

THE SPORES are monolete and bilateral with a smooth, dark brown exine and loose, densely granulose perine that is wrinkled into short, thin, sparse, lobate folds. The spores average $32 \mu \times 45 \mu$ (P \times E, exclusive of perine) and are planoconvex in lateral view and oblong in polar view. The laesura is about 30μ long and crassimarginate. Spore germination is the *Vittaria*-type (Nayar & Kaur, 1968).

THE PROTHALLIA develop basically like the *Aspidium*-type (Nayar & Kaur, 1969), and exhibit a full range of variation with respect to early formation of hairs. In the majority of cases the terminal cell of the germ filament becomes quiescent and produces a crowning unicellular hair (*Figs. 13, 14*). A lopsided prothallial plate is developed by the activity of the penultimate cells (*Figs. 15–17*). A second hair is developed on the more expanded side of the plate, and this is usually followed by the establishment of a lateral meristematic cell between the two hairs. The growing apex of the prothallus soon becomes symmetrical, with a median meristematic cell (*Fig. 18*). Many thalli omit a meristematic cell stage. In a few cases hair formation is rather delayed during prothallial development, and a prothallial plate is formed by the activity of the terminal cell of the germ filament (*Figs. 15A, 16A*). In such cases the young prothallial plate is symmetrical and naked. Soon, however, a terminal hair develops on the plate and the plate becomes asymmetric due to unilateral growth. The prothalli become distinctly cordate about 40 days after spore germination. A pluricellular meristem replaces the meristematic cell (or in thalli which skip the meristematic cell stage, a meristem is established directly from anterior marginal cells) when the apex

of the thallus becomes cordate (*Figs. 19, 20*). Young thalli are profusely hairy. The hair-bearing marginal cells frequently become protruded and sometimes form short protuberances two cells long, making the prothallial margin irregular (*Fig. 20*).

The prothalli reach maturity about 60 days after spore germination. The adult prothallus (*Fig. 21*) is of the common, cordate-thalloid type; it is symmetrical, nearly circular, 6–7 mm across, and has a median midrib 6–8 cells thick, and broad, flat wings. The wing cells possess collenchyma-like thickenings at the corners (*Fig. 24*). Unicellular papillate hairs are profuse all over the thallus; the hair-bearing marginal cells are prominently protruded. The hairs are thin-walled, chlorophyllous (with chloroplasts markedly smaller than those in other prothallial cells), and secretory, the secretion forming a prominent, tough, waxy cap crowning the hair (*Fig. 22*). In addition, all the adult prothalli (not some of them only, as Loyal (1960) reported) bear profuse, much elongate, rhizoid-like hairs (“bristles”) on the anterior margin and surfaces. These are thin-walled, unicellular (*Figs. 23, 26*), and sparsely chlorophyllous like the papillate hairs, but are several times longer, more highly vacuolated, and devoid of any secretion. Occasionally both types of hairs have one or two transverse septae in their basal half. Hairs intermediate in size between papillate hairs and rhizoid-like hairs also occur, and these commonly have a scanty secretion. “Acicular hairs similar to those on the lamina of fronds” that Loyal (1960) reported were not found on the prothallus.

Sex organs are of the common type found in advanced leptosporangiate ferns. The antheridium is subglobose with a funnel-shaped basal cell (*Fig. 25*). The cap cell collapses at antheridial dehiscence. The archegonial neck is slender and curved away from the apex of the prothallus; the neck is not straight, as Loyal (1960) reported. The neck canal cell is binucleate and swollen toward the tip at maturity.

DISCUSSION

The peculiar combination of common taxonomic characters in *Hypodematum* has rendered the genus phylogenetically ambiguous. It is associated with the woodsoid ferns by Copeland (1947),

the thelypteroid ferns by Ching (1933, 1935, 1940, 1963), the athyrioid ferns by Loyal (1960), and the tectarioid ferns by Holttum (1954) and others. The acicular foliar hairs and paired leaf traces are construed as indicative of thelypteroid affinity, the general morphology of the lamina and its resemblance to *Lastreopsis* as indicative of tectarioid affinity, and the paired leaf traces and basic chromosome count ($n = 41$) as indicative of athyrioid affinity. The chromosome count alone seems sufficient to rule out a thelypteroid relationship, despite the acicular foliar hairs of the thelypteroid type on *H. crenatum*. *Hypodematum* includes species which lack acicular hairs, and so this feature should not be given much weight in phyletic considerations, as Iwatsuki (1964a, b) pointed out. Also, characteristically the paleae of thelypteroid ferns also bear acicular hairs, which are absent in *H. crenatum*, the paleae of which bear instead papillate hairs both on the margin as well as on the surface, as in some of the dryopteroid and athyrioid ferns. The prothalli of thelypteroid ferns have *Drynaria*-type development, in contrast to the *Aspidium*-type characteristic of *Hypodematum* and the dryopteroid and tectarioid ferns. At the same time, *Hypodematum* cannot be held as closely related to the latter groups, mainly because of its binary leaf trace with broad, ribbon-like vascular strands. Both the dryopteroid and tectarioid groups have a large number of slender, cylindrical vascular strands constituting their leaf trace. In addition, the prothallial trichomes, particularly the unique, elongate, rhizoid-like, non-glandular hairs of *Hypodematum*, have no parallel in any of these ferns. The tectarioid ferns, as far as known, possess a few branched, club-shaped glandular hairs on their prothalli, in addition to papillate secretory hairs. The woodsoid as well as the dryopteroid ferns have only papillate hairs. *Hypodematum* resembles the athyrioid ferns in having paired leaf traces and two ribbon-like vascular strands in the stipe, but differs in its characteristic stelar architecture of the rhizome and more significantly in its prothallial morphology; the athyrioid ferns have a *Drynaria*-type, not an *Aspidium*-type, of development.

Hypodematum, therefore, cannot be held to belong to any of the

groups of ferns with which it has been associated in the past by different pteridologists. However, there is little reason to doubt that it is most closely allied to the Dryopteridaceae, as is amply proved by spore and prothallus morphology and chromosome number. That it is an evolutionarily advanced genus is evident from its stelar morphology. It seems clear that the stelar cylinder with leaf gaps restricted to the dorsal surface is derived from a typical dictyostelic condition by displacement of the ventral leaf gaps in response to the peculiar habit of the plant (growing wedged in crevices of hard rock and firmly attached to the substratum), and is not a primitive condition, as suggested by Iwatsuki (1964b). That the ancestral condition is a radially symmetrical dictyostele is indicated by the presence of such a vascular cylinder at the bases of rhizome branches, which gradually progresses to the fully developed form by displacement of ventral leaf gaps. The presence of suppressed leaves on the rhizome is another such indication. It is only the lateral leaves towards the ventral surface that are suppressed, and not any of the median ones. Occasional suppression of some of the ventral leaves and displacement of ventral leaf gaps towards the dorsal surface occur in some genera of the Dryopteridaceae which include some species with erect rhizomes and others with creeping or semi-erect rhizomes, like *Polystichum* (Chandra, 1969) and *Tectaria*. A similar suppression of ventral leaves is encountered also in the creeping species of *Oleandra* (Nayar et al., 1968). Also, the leaf gaps of *Hypodematium* exhibit a distinct spiral arrangement on the stelar cylinder; they are not in two or three dorsal, longitudinal rows, as described by Mehra and Loyal (1956) and Iwatsuki (1964a, b). A unique feature of *Hypodematium* is its branch traces, which are solid, superficial strands on the ventral surface of the rhizome and resemble root traces. Such branch traces are not reported in any other fern with which *Hypodematium* has been associated. They recall the stolons produced by *Nephrolepis*.

It seems best to regard *Hypodematium* as an isolated genus in the Dryopteridaceae, as suggested by Nayar (1970). It represents a line of evolution coordinate with the dryopteroid, athyrioid,

and tectarioid ferns, but distinct from them. The latter three groups and *Hypodematum* each may be considered a subfamily of the Dryopteridaceae.

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Shorter Note

PYRROSIA PRINCEPS, A FERN NEW TO CULTIVATION.—I have recently received for identification from Mr. J. W. Peterson an unidentified fern that is being cultivated in Longwood Gardens from material collected by R. G. Wilson in New Guinea and Bougainville (*Peterson J-1087*, collected Jan. 12, 1970). It proves to represent a species previously unknown in cultivation and very restricted in its natural distribution:

PYRROSIA **princeps** (Mett.) Morton, comb. nov.

Polypodium princeps Mett. *Ann. Lugd. Bat.* **2**: 232. 1866. TYPE: New Guinea, *Zippel* (holotype L, Morton photograph 833).

Cyclophorus princeps (Mett.) C. Chr. *Ind. Fil.* 200. 1905.

This is a characteristic species, known to me from only three collections (aside from the type) from New Guinea: Auga River, in clumps among rocks near river, alt. 580 m., Papua, Sept.-Nov., 1933, *Brass 5492*; terrestrial in edge of forest on riverbanks, Biniguni Camp, Gwariu River, Milne Bay District, Papua, July 30, 1953, *Brass 23703*; on limestone cliffs, Biak Island, December 2, 1945, *Grether & Wagner 4220*. From the data on the label of the cultivated plant it appears that the species may occur also on Bougainville Island, Solomon Islands.

In habit this species is quite different from the commonly cultivated *Pyrrrosia lingua* (Thunb.) Farwell, which has long-stalked fronds scattered along an elongate, creeping rhizome. The rhizome is compact and larger in *P. princeps*, and the fronds are fasciculate. The fronds are probably the largest in the genus *Pyrrrosia*, reaching more than a meter in length and 10 cm. in